IRON ABSORPTION IN DIFFERENT PLANT SPECIES AS A FUNCTION OF THE pH VALUE OF THE SOLUTION

BY

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INTRODUCTION

It is a well-known fact that the hydrogen ion concentration of the soil is a significant factor governing the distribution of plants in nature: each plant species is found only in soil having a pH value within a range characteristic of the species in question (OLSEN 1923).

Certain species (acid soil plants) occur only in soil of a pH between 3.6 and 5.0. Other species (basic soil plants) grow only in soil of a pH between 6.0 and 8.0. Comparatively few species are definite acid soil plants, while numerous species belong to the group of basic soil plants. Furthermore there are some species that are found in strongly acid as well as slightly acid, neutral, or slightly alkaline soil. Cultivation experiments with several of these species (*Spergula arvensis*, *Rumex acetosella*, *Convallaria majalis*, *Majanthemum bifolium*) have shown that they grow equally well in soils with pH values covering the range from 4.0 to 8.0 (OLSEN 1936).

Water culture experiments with typical acid soil plants and basic soil plants have shown that the plants respond to the pH value of the solution in much the same way as to the pH of the soil. In solutions of pH values between 4.0 and 5.0, *Deschampsia flexuosa* shows optimum growth. When the pH increases growth slows down, and in solutions within the pH range 6.0 to 8.0 chlorosis and pronounced inhibition of growth are observed (OLSEN 1938). *Sinapis alba* shows optimum growth in solutions of pH 6.0 to 8.0. In the pH range from 4.0 to 6.0 growth is inhibited, and in solutions of pH 4.0 or lower this plant species cannot develop at all (OLSEN 1935). In contradistinction to these two species, a plant like rye (*Secale cereale*) proves indifferent to the pH value of the solution in so far as it shows optimum growth in solutions covering the entire range from 4.0 to 8.0. It has been demonstrated that hydrogen ions are only directly harmful to rye plants at pH values of 3.5 or lower, while direct harmful effects of hydroxyl ions occur only at pH values around 10.5 or higher (OLSEN 1953).

This raises the following questions: Is the inhibition of growth observed in *Deschampsia flexuosa* when the pH of the solution is increased from 6.0 to 8.0 due to the rise in hydroxyl ion concentration? And conversely, is the increasing growth inhibition observed when *Sinapis alba* is cultivated in solutions of pH values decreasing from 6.0 to 4.0 caused by the increasing hydrogen ion concentration? Neither assumption seems probable. The fact that it has not until now proved possible to make either acid soil plants or basic soil plants develop to the optimum extent in solutions of arbitrary pH values within the range from 4.0 to 8.0, is hardly due to the pH in itself, but to other factors which, under the experimental conditions hitherto employed, vary concurrently with the pH value. In soil these factors are inextricably bound to the pH value and cannot be altered independently, but in solution culture this might be possible. That it actually is so will be seen from the experiments described in the following.

METHODS

As nutrient solution a four-salt solution was used; it contained three cations and three anions in the concentrations indicated in Table 1.

Table 1.

Composition of the nutrient solution.

Per liter	m.eq. per liter					
	K	Ca	Mg	NO_3	H_2PO_4	SO_4
0.354 g $Ca(NO_3)_2$, $4H_2O$	..	3.0	...	3.0	..	..
0.370 g $MgSO_4$, $7H_2O$	..	..	3.0	..	..	3.0
0.270 g KNO_3	2.67	..	..	2.67	..	..
0.046 g KH_2PO_4	0.33	..	..	..	0.33	..
Total...	3.0	3.0	3.0	5.67	0.33	3.0

Glass-distilled water was used. In addition to the four salts listed in Table 1, the solution contained trace elements. The amounts of their compounds per liter were 1 mg $MnSO_4$, $4H_2O$ — 0.8 mg H_3BO_3 — 0.2 mg $ZnSO_4$, $7H_2O$ — 0.05 mg $CuSO_4$, $5H_2O$ — 0.05 mg

$(NH_4)_6Mo_7O_{24}, 4H_2O$. Iron was added either as ferric sulfate or as iron versenate; in either case the concentration was 0.5 mg Fe per 1.

The iron versenate solution was prepared by dissolution of 2.61 g Complexone II (ethylenediaminetetraacetic acid, Siegfried) in 26.8 ml 1*M* KOH, addition of 2.49 g $FeSO_4, 7H_2O$, dilution to 100 ml, and aeration for twenty-four hours.

Each nutrient solution was adjusted to the desired pH value by addition of sulfuric acid or potassium hydroxide. The plants were cultured in glass cylinders 20 cm high by 19 cm wide, each containing five liters of nutrient solution. The vessel was covered with a galvanized iron plate with four holes. A plant was placed in each of these holes, supported by a flat, perforated cork. The solution was aerated with a continuous stream of air throughout the experimental period.

The contents of iron, calcium, magnesium, and potassium in the plants were determined by methods previously described (Olsen 1934, 1939, and 1942).

Experiments with *Deschampsia flexuosa.*

Deschampsia flexuosa (bent grass) grows on waste land and in forests on raw humus. It occurs frequently on soil having pH values from 3.5 to 5.0, but not above 5.0 (Olsen 1923). If it is sown on soil of pH values in the range 4.0 to 8.0 it develops most vigorously at pH values between 4.0 and 5.0, but growth declines rapidly above pH 5. In soil of pH values from 6.0 to 8.0 the germinating plants soon become chlorotic and then do not develop further (Olsen 1923, 1936, 1938 II). In solution cultures the plants have behaved in the same way in all experiments previously reported: Already in solution of pH 6.0 definite chlorosis is observed, and at pH 7.0 no growth occurs at all (Olsen 1923, 1938 II). It is certain that the chlorosis is due to iron deficiency. In previous investigations into chlorosis in corn plants, conspicuous in solution of pH 7.0, it was found (Olsen 1935) that chlorosis could be avoided when iron was added to the neutral solution as ferric citrate, in which the iron is bound in complex form. Later (Olsen 1938 II) a number of *D. flexuosa* experiments were performed in which the composition of the solution was varied in several ways. Although ferric citrate was used as source of iron, it did not prove possible to make the plants develop in solutions of pH 7.0 or 8.0.

First in 1957 new experiments were undertaken with *D. flexuosa*. In place of ferric citrate, which is rather unstable in solution, ferric versenate (an iron compound of ethylenediaminetetraacetic acid) was used. This compound contains its iron in very stable chelate binding; in numerous cases it has proved an excellent iron source for plants in solution culture. It has been used by the present author as iron source for *Helodea canadensis* (OLSEN 1954).

Small plants of *D. flexuosa* were collected from their natural habitat and precultured in the above solution at pH 4.0 and with ferric sulfate as iron source. After about one month the plants had formed vigorous new roots; now they were transferred to the vessels used for the growth experiments proper. Their initial weight of dry matter was ca. 3 g per vessel holding four plants. The plants were cultured in solutions of pH 4.0 and 7.0, respectively. At each pH value ferric sulfate was used as iron source in some experiments, iron versenate in others. The experimental period was a little more than four months (January 3 to May 9, 1957). The cultures stood in a greenhouse where the temperature was maintained between 15 and 20° C. During the first three months they were illuminated by means of fluorescent lamps. During the experimental period the solutions were changed eight times. Their pH values were checked daily; whenever the pH of a solution differed more than 0.2 from its specified value, it was corrected by dropwise addition of 1 molar sulfuric acid or potassium hydroxide.

The plants having iron versenate as source of iron grew vigorously with a considerable increase in dry matter. This was true in solution of pH 7.0 as well as at pH 4.0 (Table 2); in both solutions the leaves were a deep green.

The plants grown on ferric sulfate as iron source likewise developed vigorously at pH 4.0, but in solution of pH 7.0 the plants soon grew chlorotic (Plate I), and after termination of the experiment the increase in dry matter proved to be only one-ninth of that of the plants cultured at the same pH, but with iron versenate as source of iron (Table 2).

Table 2 further shows that the relative iron content is least in the leaves of the chlorotic plants. The chlorosis is not only caused by the fact that the plants cannot take up sufficient quantities of iron from the solution, but also by difficulties in internal translocation, the iron being precipitated in the veins so that it is unable to pass into the mesophyll. This has been shown in previous experiments with corn plants (OLSEN 1935) and has been confirmed by REDISKE and BIDDULPH (1953) in experiments on *Phaseolus vulgaris*.

Table 2.

Deschampsia flexuosa in nutrient solution.

pH of solution	Iron source	Increase in dry matter[1], g	mg per g leaf dry matter Fe	Ca	Mg	K
4.0	Ferric sulfate	33.4	0.13	3.1	1.17	22.1
	Iron versenate	32.1	0.15	3.5	1.30	24.2
7.0	Ferric sulfate	3.6	0.10	12.4	4.88	55.0
	Iron versenate	31.6	0.16	4.0	1.93	22.3

[1] The increase in dry matter is taken as the weight of dry matter of four plants at the end of the experiment minus 3.0 g (the dry matter of four plants at the beginning of the experiment).

Furthermore, Table 2 shows that the contents of calcium, magnesium, and potassium in the leaves of the chlorotic plants are almost three times those in the leaves of the normal, green plants. Previous experiments (OLSEN 1935) showed chlorotic corn plants to contain far more calcium, magnesium, and potassium than normal, green corn plants. This must presumably be explained by the assumption that, whereas the dry matter production of the chlorotic plants soon slows down, the uptake of salts from the solution continues so that the inorganic constituents become associated with a smaller quantity of dry matter than in the normal, green plants.

Finally, Table 2 shows that, apart from the chlorotic plants, the calcium content of the leaves of the experimental plants is very low, viz. ca. 3.5 mg Ca per g dry matter. When *Cannabis sativa* was grown in the same solution, in which calcium, magnesium, and potassium were present in equivalent concentrations, its leaves contained 48.0 mg Ca per g dry matter, or about fourteen times as much as *D. flexuosa*. The low calcium uptake is characteristic of *D. flexuosa*. It is seen from Table 3 that the calcium content of the leaves is still lower in the natural habitat of this plant, while the contents of potassium and iron are not very different from those in the experimental plants. The extremely low calcium content in the leaves from the natural localities is of course a consequence of the very low calcium concentration of the strongly acid raw humus.

If the Tables 2 and 3 are recalculated as equivalents it will be seen that the Ca/Mg ratio is ca. 1.5 in the leaves of the experimental plants, but only 0.67 in the leaves of the plants from the natural habitat. In other words, there is relatively more magnesium than calcium in the plants from the raw humus, and this must be due to

Table 3.

Contents of Fe, Ca, Mg, and K in leaves of *D. flexuosa* taken from two different localities on the Danish island of Zealand; mg per g dry matter.

	Fe	Ca	Mg	K
Gribskov...............	0.13	1.12	1.01	20.4
Gyldenløveshøj	0.14	1.24	1.13	15.3

the fact that this strongly acid soil contains relatively more accessible magnesium than calcium.

The main result of the experiments is that *D. flexuosa* can attain optimum growth in solution culture throughout the pH range 4.0 to 8.0 when iron is added as iron versenate. When ferric sulfate is the (sole) iron source the plants grow chlorotic in solutions of pH 6.0 to 8.0, and the production of dry matter ceases.

Similar conditions prevail in soil, and the reason why *D. flexuosa* cannot grow in soil at a pH above 6.0 is the fact that it is unable to absorb a sufficient quantity of iron.

Experiments with ***Cannabis sativa*** and ***Secale cereale***.

Figure 1 shows hemp growing in soils of pH values 4.0, 5.0, and 7.0, respectively. It will be seen that the optimal pH for growth of hemp is in the neighbourhood of 7. In soil of pH 4 the plant is almost unable to grow, and in soil of pH 5 growth is considerably retarded.

In some studies of competitive ion absorption commenced in 1955, hemp (*Cannabis sativa* var. *gigantea*) and rye were used as experimental plants. The latter is a typical pH-indifferent species. Originally it was not intended to study the responses of the two species to the pH values of the solutions, the author having no notion at the time that hemp was a typical "basic soil plant". The reason why hemp was introduced was the known fact that, in contrast to rye, hemp had an extraordinarily high rate of calcium absorption.

Both plant species were grown in solutions containing six different concentrations of calcium ranging from 0 to 30 m.eq. per l. The solutions had the composition given in Table 1 except for the calcium nitrate. Iron was added as ferric sulfate; the other trace elements were unchanged. The pH was kept constant at 5.0 since this value had proved favorable in experiments with rye. This soon proved not to be true in the case of hemp, and just this fact made it possible

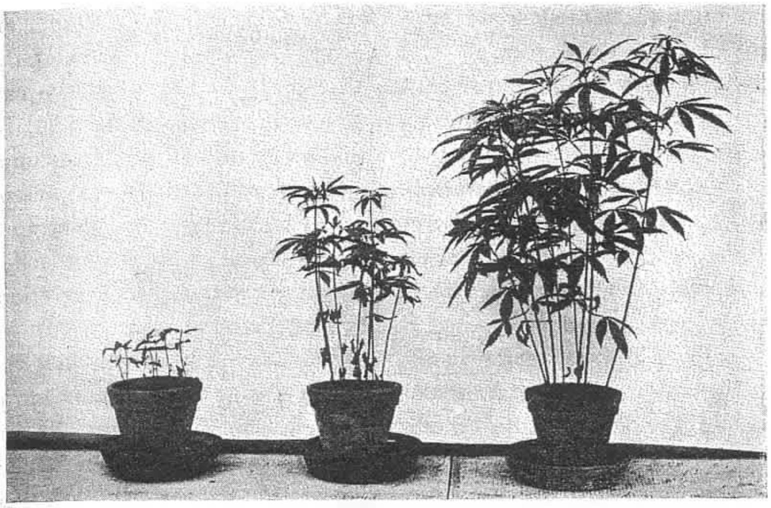
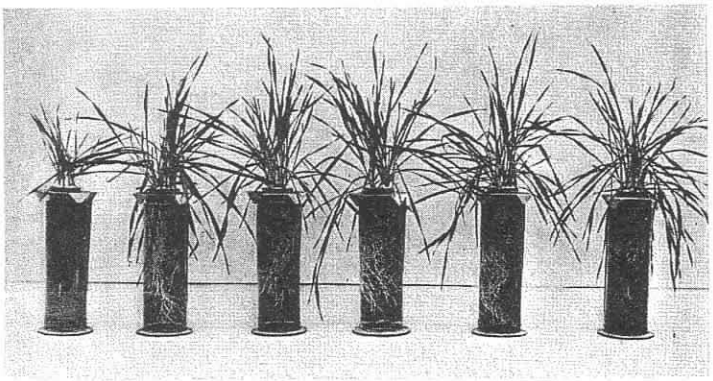


Fig. 1. Hemp in soils of different pH values. The soils in the left and middle pots were forest soils, that in the right pot garden soil. To all the pots identical quantities of potassium nitrate and potassium dihydrogen phosphate were added. The plants were transplanted as seedlings.

to obtain information concerning the peculiar behaviour of hemp in acid solutions.

When the experiments had lasted four weeks, the plants were photographed, dried, and weighed, and their contents of calcium, magnesium, and potassium were determined.

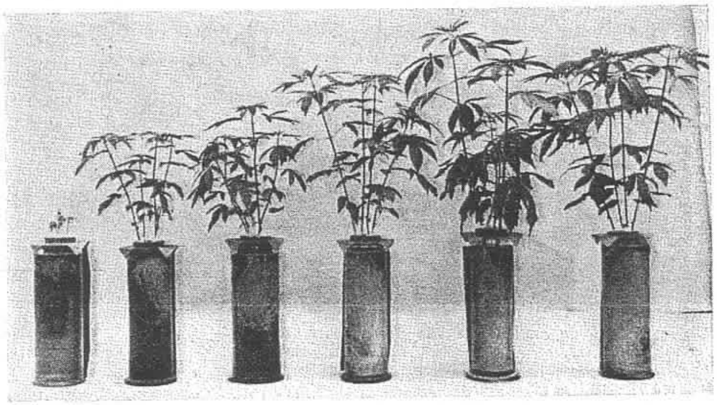


m.eq.Ca/l	0	0,5	1.0	3.0	10.0	30.0
Dry matter, g	1.4	4.1	4.4	4.5	4.4	3.8

Fig. 2. Rye in solutions of increasing calcium concentration. pH 5.0 throughout.

Figure 2 shows the rye plants. Below each plant the calcium content of its nutrient solution and the dry weight of the plant at the conclusion of the experiment are stated. It is seen that rye can develop to a certain extent even in a solution devoid of calcium. To be sure, the plants grown in such a solution were not free of calcium; four plants contained a total of 0.85 mg Ca, which had been present in the seedlings before they were placed in the solution. Even in a solution containing only 0.5 m.eq. Ca per 1 the dry weight approached the optimum. On the other hand, the highest calcium concentration, viz. 30 m.eq. per 1, decreased the dry weight somewhat.

Figure 3 shows hemp in the same solutions. It is seen that the dry weight increased throughout with increasing calcium concentration in the solution. In calcium-free solution the plants did not develop at all. In the solution containing 0.5 m.eq. Ca per 1, where the dry weight of rye approached the optimum, the dry weight of hemp was only one-fourth of that attained by the plants growing at the highest calcium concentration. This experiment might lead one to the conclusion that hemp required large amounts of calcium for optimum development, which would be in accord with the views of the botanists of the nineteenth century, who thought that plants growing preferentially on calcareous soil required large quantities of calcium (SCHNITZLEIN and FRICKHINGER 1848). However, the situation is not so simple. The well-known symptoms of calcium deficiency,



m.eq. Ca/l	0	0.5	1.0	3.0	10.0	30.0
Dry matter, g	0.2	2.5	3.7	8.2	9.7	10.4

Fig. 3. Hemp in solutions of increasing calcium concentration. pH 5.0 throughout.

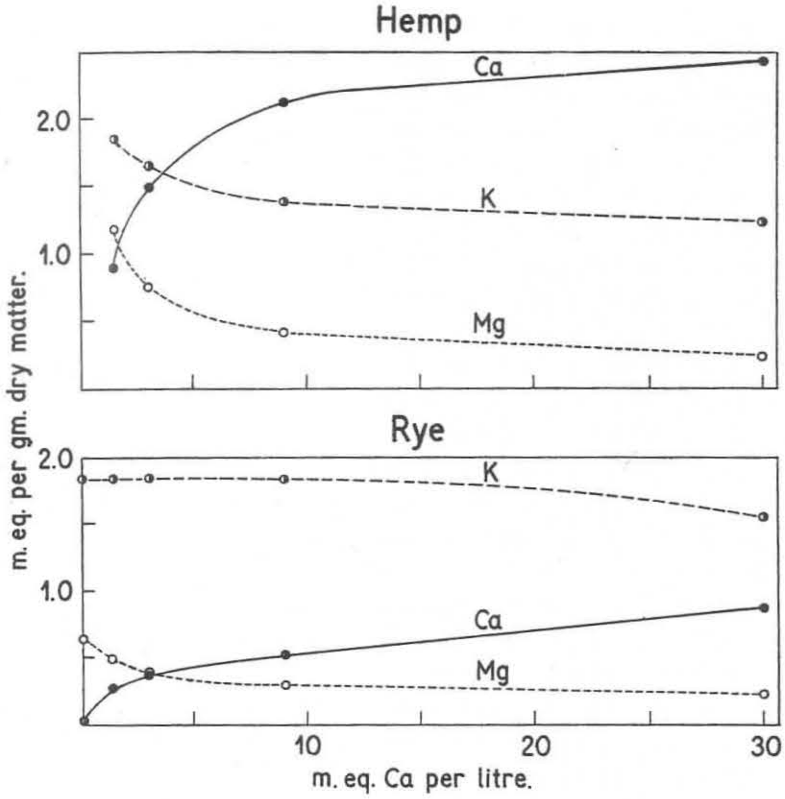


Fig. 4. The calcium, magnesium, and potassium contents of hemp and rye grown in solutions of increasing calcium concentrations. pH 5.0 throughout. Roots, stems, and leaves were analyzed separately, and the total content of each ion in four plants was calculated. The numbers in the figures represent the total content divided by the weight of dry matter.

such as dying of growing points, were not observed in the feebly developed hemp plants, so that there was no reason to believe that the growth inhibition in the solutions of low calcium content was due to shortage of calcium. More probably it was caused by a toxic effect of one or more cations of which too much was absorbed. In a solution of high calcium ion concentration the absorption of the other cations present is depressed as a result of competition, and the toxic effect is alleviated.

The results of competition between cations in hemp and rye are shown in Figure 4, which shows the contents of calcium, magnesium, and potassium in the plants at the termination of the experiment.

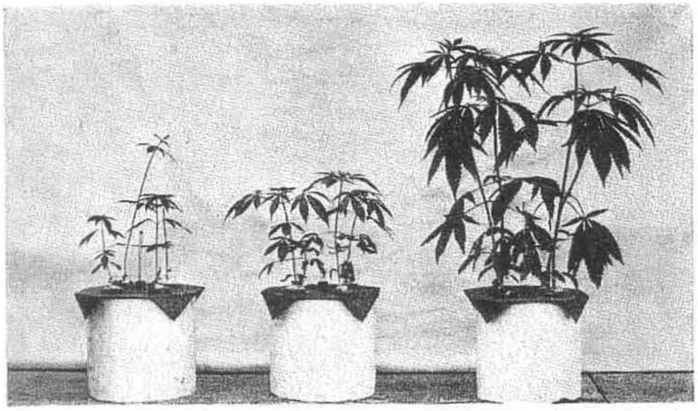
When the calcium concentration in the solution was increased, both plant species absorbed increasing quantities of calcium. At the same time the uptakes of magnesium and of potassium went down, particularly that of magnesium, since competition is always more pronounced between more closely related ions, in the present case the two divalent cations. Furthermore, the figure shows that there was a characteristic difference between hemp and rye in that hemp absorbed three to four times as much calcium as did rye, and also more magnesium. However, the Mg/Ca ratio was higher in rye. There was no marked difference in the quantities of potassium taken up.

Now the question is: Which of the cations present in the solution inhibits the growth of hemp when the calcium ion concentration is low? Some experiments that will not be described in detail here showed that the magnesium ion concentration could be increased considerably relative to the calcium ion concentration without affecting the development of the hemp plants. Hence the toxic ion could not be the magnesium ion. Attention was now directed to the trace elements. It was found that a considerable increase of the concentrations of manganous and zinc ions in a solution containing 10 m.eq. Ca per 1 caused no growth inhibition, while a considerable decrease of these ions in a solution containing 1 m.eq. Ca per 1 did not abolish the inhibition. So neither the zinc nor the manganous ion was toxic. This made it probable that the toxic effect was due to the ferric ions present.

An increase in the concentration of ferric ions, with a view to enhancing the growth inhibition, could only be effected by lowering the pH of the solution since the ferric ion concentration attainable was limited by the solubity of ferric hydroxide. In the above experiments the pH had been 5.0; it was now lowered to 4.0.

Figure 5 shows the result of an experiment with hemp in solution of pH 4.0 containing ferric sulfate as source of iron; the contents of calcium and magnesium were varied. It is seen that when the calcium ion concentration was sufficiently high, viz. 10 m.eq. per 1, hemp developed quite normally even in solution of pH 4.0. If the calcium concentration was decreased to 1 m.eq. per 1, growth inhibition occurred, and if both the magnesium and the calcium concentrations were reduced to 1 m.eq. per 1, the inhibition was enhanced; this may be ascribed to reduction of the competitive effect of the magnesium ions. The plants exhibited distinct symptoms of intoxication.

The intoxicated plants had small, deep green leaves containing



m.eq. Ca/l	1	1	10
m.eq. Mg/l	1	3	3

Fig. 5. Hemp in solutions of pH 4.0 with ferric sulfate as iron source. The concentrations of calcium and magnesium in the solutions were varied.

as much as 1.3 mg iron per g dry matter, which is about four times as much as found in leaves of normal plants. The roots were short and ramified in a way that was reminiscent of corals; they had no root hair. Growth soon came to a standstill, no fresh leaves or roots developing. Hemp seedlings planted into soil of pH 4.0 soon showed the same symptoms: deep green leaves of a high iron content, short, coral-shaped roots, and soon cessation of growth.

If iron was omitted from the solutions, the intoxication symptoms did not occur: The plants developed normally forming long, white roots. However, growth soon ceased because of iron deficiency.

The experiment of Figure 5 did not prove directly that the intoxication of the plants in the solution containing 1 m.eq. Ca per 1 was due to an excessive uptake of ferric ions. The toxic effect might be due to the hydrogen ions, and a high concentration of calcium ions might have an antagonistic effect sufficient to counterbalance the toxicity of the hydrogen ions. But the following experiment showed that this was not the correct explanation. It proved possible to obtain normal, vigorous plants in solution of pH 4.0 even when the concentrations of calcium and magnesium were only 1 m.eq. per 1. This was effected simply by replacing the ferric sulfate in the solution by iron versenate so that the concentration of free ferric ions became extremely low. Figure 6 shows the result of an experiment in which all the plants had grown in solutions containing 1 m.eq. Ca, 1 m.eq.

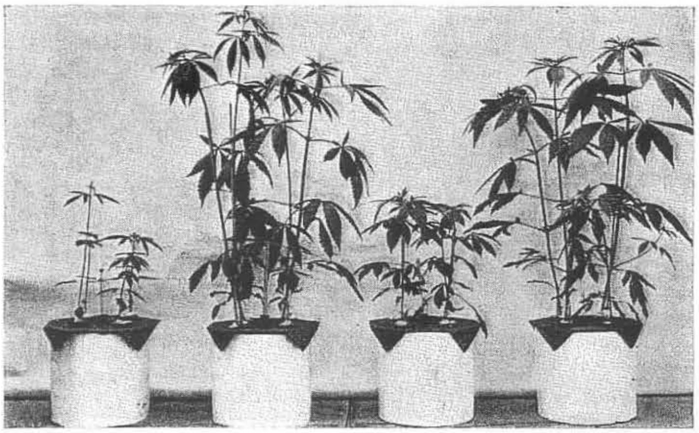


Fig. 6. Hemp in solutions of pH 4.0 and 7.0 with ferric sulfate or iron versenate as iron source. Concentrations of calcium and magnesium both 1 m.eq. per l throughout.

Mg, and 0.5 mg Fe per l. In solution of pH 4.0 the plants were intoxicated when the iron source was ferric sulfate, but when it was iron versenate normal, vigorous plants developed. This experiment clearly showed that the intoxication was due to the ferric ions. In solution of pH 7.0 the plants that had ferric sulfate as iron source were feebly developed owing to iron deficiency caused by the very low solubility of ferric iron in solution of pH 7.0. The plants that had been given iron versenate were vigorous and had developed normally.

Thus, when ferric sulfate was the iron source, the plants were intoxicated in solution at pH 4.0 because they absorbed too much iron, but in solution of pH 7.0 growth was inhibited because an insufficient amount of iron was available to the plants.

With iron versenate as source of iron the plants developed normally and grew just as well at pH 4.0 as at pH 7.0 even when the concentrations of calcium and magnesium were low.

When, as in the experiment illustrated in Figure 7, the concentrations of calcium and magnesium were high, viz. 10 m.eq. Ca and 3 m.eq. Mg per l, it proved immaterial whether iron was added to the solution as ferric sulfate or as iron versenate as long as the pH was 4.0. In both cases vigorous, well-developed plants were obtained. In solution of pH 7.0 well-developed plants were obtained only with iron versenate as source of iron, just as in the experiment of Figure 6.

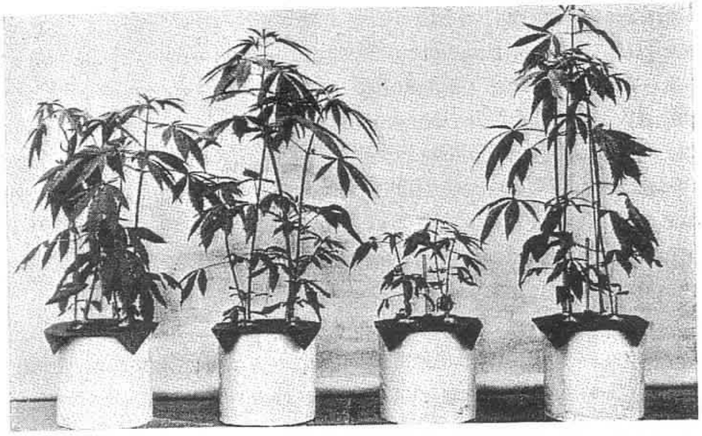


Fig. 7. Hemp in solutions of pH 4.0 and 7.0 with ferric sulfate or iron versenate as iron source. Concentration of calcium 10 m.eq. per l, of magnesium 3 m.eq. per l.

When the iron source was ferric sulfate the plants suffered from iron deficiency, and even more so than in the previous experiment, because competition was keener when the calcium and magnesium concentrations had been raised.

It might seem strange that when hemp is grown in solution of pH 7.0 with ferric sulfate as source of iron, it suffers from iron deficiency, which it usually does not when growing in soil of pH 7.0.

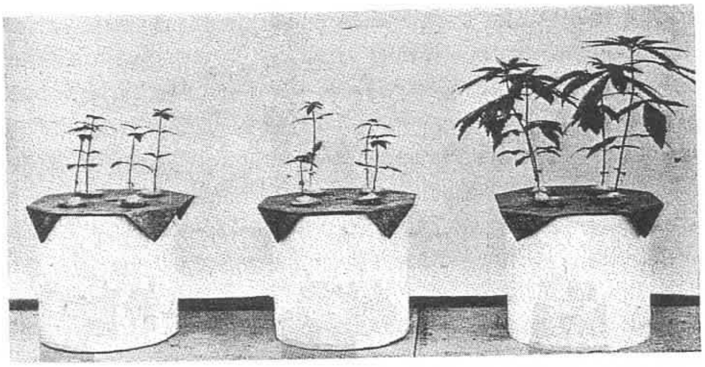


Fig. 8. Hemp in solution of pH 4.0. Calcium and magnesium concentrations 1 m. eq. per l. The plants to the left had ferric sulfate as iron source, those to the right iron versenate, those in the middle both ferric sulfate and iron versenate.

The deficiency is due to the fact that more than 99 per cent of the iron added is present as ferric hydroxide forming a sediment at the bottom of the vessel containing the nutrient solution. When the plants have absorbed the iron remaining in solution, the ferric hydroxide dissolves only very slowly. However, previous experiments with corn (*Zea mays*) (OLSEN 1938) have shown that it is possible to provide a sufficient quantity of iron in solution at pH 7.0 if the amount of precipitate is increased and if it is kept in suspension by very vigorous stirring.

In a final experiment (Figure 8), hemp was grown in solution of pH 4.0 and with low calcium and magnesium concentrations. As expected, the experiment shows that iron intoxication cannot be prevented by addition of iron versenate when the solution contains ferric ions.

DISCUSSION

The experiments show that *Deschampsia flexuosa* and hemp can attain optimum growth in solution throughout the pH range 4.0 to 8.0 when iron is added as iron versenate.

If ferric sulfate is employed as source of iron, *D. flexuosa* cannot develop in solutions of pH higher than 6.0; the plants grow chlorotic and the production of dry matter ceases because of iron deficiency. In solutions of low calcium concentration and with ferric sulfate as source of iron, hemp shows increasing growth inhibition due to iron intoxication when the pH values of the solutions decrease from 6.0 to 4.0. In this pH range the ferric ion concentration of the solution increases greatly when the pH falls as shown by Figure 9. It will be seen that the nutrient solution used in the experiments (Table 1) can only contain 0.002 mg ferric ion per l in stable solution at pH values above 6.0. However, when the pH decreases from 6.0 to 4.0, the solubility of ferric iron increases considerably, and this causes the rate of iron absorption to rise as long as the concentration is below 0.003 m.eq. (= 0.056 mg) Fe^{+++} per l (OLSEN 1950).

With ferric sulfate as iron source, hemp can develop quite normally even in solution of pH 4.0 if the calcium concentration is raised to 10 m.eq. per l so that the Fe/Ca ratio is diminished. The competition between the calcium and ferrric ions causes the rate of iron absorption to decrease so far that intoxication does not occur.

It is difficult to say anything about the mechanism of iron intoxication. As mentioned above the leaves of the intoxicated plants

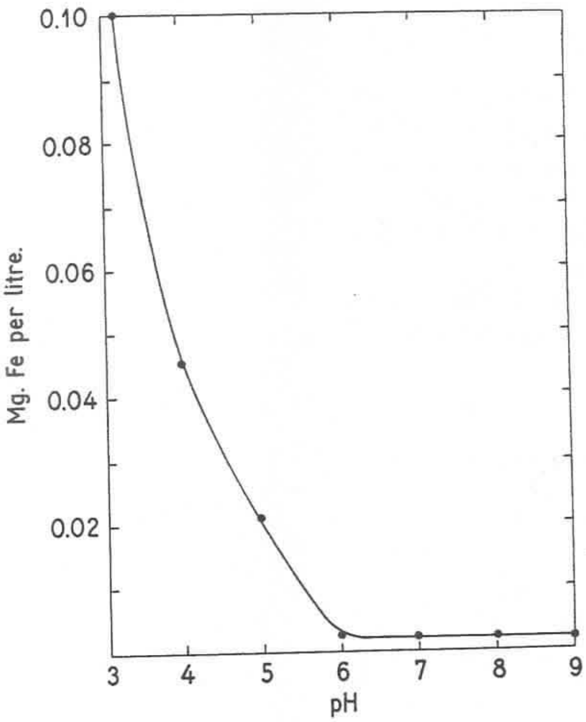


Fig. 9. Ferric ion concentrations (as mg Fe per l) in nutrient solutions as a function of the pH value.

contain as much as 1.3 mg Fe per g dry matter, which is about four times as much as in leaves of normal plants. In roots of intoxicated plants iron contents as high as 8.0 mg per g dry matter have been found. However, these data are not a true expression of the real iron contents of the roots because an appreciable proportion of the iron is present as ferric hydroxide adhering to the surface. In the intoxicated plants water absorption was inhibited. This was shown by the fact that their leaves grew flaccid and drooping when the temperature of the greenhouse rose; this did not occur in normal plants.

Sinapis alba has previously been used by the author as an example of a basic soil plant. In a few experiments done in 1956 it behaved just like hemp. In solution of pH 4.0, with a low calcium content, and with ferric sulfate as iron source, the *S. alba* seedlings developed into small, deep green plants, which soon ceased to grow because of iron intoxication. The intoxication could be avoided either by the use of iron versenate as source of iron or by increasing the calcium concentration of the solution to 10 m.eq. per l. In both cases normal, well-developed plants were obtained.

When rye is grown in solution of pH 4.0 and with a low calcium content, normal, well-developed plants appear when the iron source is ferric sulfate, but still the production of dry matter is increased somewhat if iron versenate is used in place of ferric sulfate. This shows that rye is not quite unsusceptible to iron intoxication although its susceptibility is much less than that of hemp.

The difference is presumably a reflection of the difference in the rates at which the two plant species absorb ferric ions. Rye absorbs slowly, hemp considerably more rapidly.

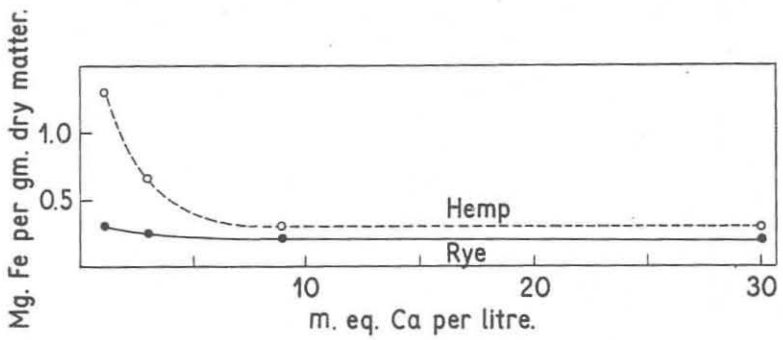


Fig. 10. The iron contents of leaves of hemp and rye grown in solutions of four different calcium concentrations. The pH value was 4.0 throughout.

This is seen from Figure 10, which shows that leaves of hemp that had grown in solution of pH 4.0 and a low calcium content, viz. 1 m. eq. per 1, contained four times as much iron as did leaves of rye that had grown in the same solution. The iron content in the leaves of *Deschampsia flexuosa* suggests that this plant species has a still lower rate of iron absorption than has rye. It is seen from Tables 1 and 2 that both the experimental plants and the plants that had grown in natural localities had a lower iron content in their leaves than had rye. The plants from Gribskov had grown on soil of pH 4.0 having a very low content of calcium ions, which may be seen from the extremely low calcium content of the leaves, viz. 1.12 mg Ca per g dry matter. In spite of this the iron content of the leaves is no higher than in the experimental plants, which had grown in solution containing 3 m.eq. Ca per l. This suggests that the rate of iron absorption is not, or only slightly, increased even by a great reduction of the calcium concentration in the solution (this experiment has not been done), and that consequently *D. flexuosa* is not susceptible to iron intoxication.

We have seen that the rate of iron absorption is highest in hemp, lower in rye, and presumably still lower in *D. flexuosa*. The rates of absorption of the divalent ions calcium and magnesium decrease in the same sequence: Hemp has the highest rates of absorption of these ions, *D. flexuosa* the lowest.

Thus the fact that "basic soil plants" show increasing growth inhibition with increasing hydrogen ion concentration in the soil is not directly due to the increase in hydrogen ion concentration, but to the increased solubility of iron, which, in conjunction with the low contents of calcium and magnesium, causes the plants to absorb so much iron that intoxication occurs.

Undoubtedly aluminum intoxication may contribute to making it impossible for basic soil plants to develop in strongly acid soil. The symptoms of aluminum intoxication have been known for many years (Hartwell and Pember 1918, Olsen 1923). Probably aluminum intoxication makes itself felt only at pH values of 4.0 or below, since the solubility of aluminum hydroxide is negligible at higher pH values. In contrast, iron intoxication may occur already at pH values slightly below 6.0.

SUMMARY

The acid soil plant *Deschampsia flexuosa* and the basic soil plants *Cannabis sativa* and *Sinapis alba* can attain optimum development in solution culture throughout the pH range from 4.0 to 8.0 when iron is added as iron versenate.

With ferric sulfate as source of iron *D. flexuosa* cannot develop in solutions of pH above 6.0; the plants become chlorotic and the production of dry matter comes to a standstill because of iron deficiency. The same is true in soil of pH higher than 6.0.

When hemp (*C. sativa*) and mustard (*S. alba*) are cultured in solutions low in calcium and with ferric sulfate as iron source, increasing growth inhibition due to iron intoxication is observed when the pH value of the solution decreases from 6.0 to 4.0. This is due to the fact that in this pH range the ferric ion concentration in the solution increases greatly when the pH is lowered. The same is true in soil. Thus the fact that hemp and mustard do not thrive in soil of pH values appreciably lower than 6.0 is not due directly to the

hydrogen ion concentration, but to intoxication caused by an excessive rate of iron absorption.

Even with ferric sulfate as iron source, hemp and mustard can develop quite normally in solution of pH 4.0 provided the calcium ion concentration of the solution is high. This is due to the competitive action of the calcium ions resulting in a sufficient lowering of the rate of iron absorption to preclude intoxication. This antagonistic situation does not occur in nature since soil of low pH and high calcium concentration does not exist.

In *D. flexuosa* and rye (*Secale cereale*) iron intoxication does not occur, as it does in hemp, when the plants grow in soil of pH 4.0 or in solution of this pH and low in calcium. The difference between the three plant species in this respect is probably a reflection of the difference in rate of absorption of ferric ions. *D. flexuosa* and rye absorb iron slowly, hemp a great deal more rapidly.

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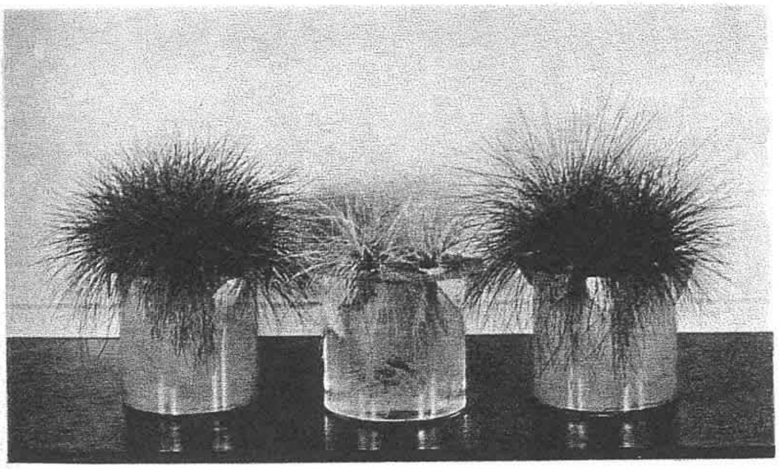
PLATE I



Deschampsia flexuosa in solution culture. The plants to the left had developed in solution of pH 4.0 with ferric sulfate as iron source. The chlorotic plants in the middle had developed in solution of pH 7.0 containing ferric sulfate. The plants to the right had developed in solution of pH 7.0, but with iron versenate as source of iron.

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